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Humpback Whale, Megaptera novaeangliae, Feeding Dynamics From the Perspective of the Individual: Insights From Demography, Life History, and Bio-Logging

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HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, FEEDING DYNAMICS FROM THE PERSPECTIVE OF THE INDIVIDUAL: INSIGHTS FROM DEMOGRAPHY, LIFE HISTORY, AND BIO-LOGGING

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ABSTRACT

HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, FEEDING DYNAMICS FROM THE PERSPECTIVE OF THE INDIVIDUAL: INSIGHTS FROM DEMOGRAPHY, LIFE HISTORY, AND BIO-LOGGING

by Jennifer Tackaberry

Studies of fission-fusion societies provide a framework in which to compare the feeding dynamics across demographics, unrestrained by stable associations or relatedness. This study used bio-logger data and surface observations combined with long-term population data from the Gulf of Maine humpback whale, *Megaptera novaeangliae,* population to investigate the influence of demographics on feeding methods, and time spent feeding, and to determine if a coordinated feeding method, kick-feeding, was a cooperative behavior. The results suggest that demographics did influence the feeding method used and highlighted the need to determine how energetic needs change across the feeding season. Adult females did not spend more time feeding than males, but engaged more often in bottom-feeding, a difference that could put them at greater risk of entanglement in fishing gear set near the substrate. Additionally, the results suggest that kick-feeding was not a form of cooperation, but rather those dynamics were a product of demographics and local population structure. This study highlights the need to account for demographics when interpreting behavior and behavioral risk from anthropogenic activities.

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Introduction

In terrestrial and marine species, the differential foraging requirements among demographics can manifest as variations in habitat use, feeding behaviors, and targeted primary prey species (Bercovitch and Berry 2017; Heide-Jørgensen et al. 2010; Cosens and Blouw 2003). A variety of factors cause foraging needs and abilities to vary among demographics, including behavioral, morphological, and physiological constraints, preventing them from effectively occupying the same niche (Jeglinski et al. 2012; Bercovitch and Berry 2017). The opportunity to compare the feeding methods and proportion of time dedicated to feeding among demographics that occupy the same niche and are not constrained by long-term, stable associations is uncommon. However, research within a fission-fusion society provides a framework to compare the feeding abilities, time spent feeding, and prevalence of cooperation across demographics while individuals are uninhibited by additional societal constraints.

In fission-fusion societies, non-kin join and split over relatively short periods and are free from the burden of compromising their needs or cooperating with others for the betterment of the group. In contrast, when societies consist of stable long-term groups of related individuals, group members must cooperate and adjust their behavior to ensure group stability and overall group fitness (Tennessen et al. 2019; Ford et al. 2011).

There has been a great deal of research about terrestrial species with fission-fusion social structures (Bercovitch and Berry 2013; Cross, Lloyd-Smith, and

Getz 2005; Smith, Memenis, and Holekamp 2007; Metheny et al. 2008; Sundaresan et al. 2007), but many well-studied marine mammal species have long-term, stable matrilineal social structures (Ford et al. 2011; Tennessen et al. 2019) or segregated by demographics by targeting different prey species or habitats (Heide-Jørgensen et al. 2010; Cosens and Blouw 2003; Jeglinski et al. 2012). However, a well-studied marine mammal species with a fission-fusion social structure is the humpback whale, *Megaptera novaeangliae*.

Humpback whales are in all of the world's oceans, and their feeding behavior has been well studied in many regions (Hain et al. 1982; 1995; Wiley et al. 2011; Friedlaender et al. 2013; Goldbogen et al. 2008; Sharpe 2001), but little is known about the influence of demographic class on the feeding methods used. Past studies have suggested that energetic needs among demographics differ (Irvine et al. 2017; Tyson et al. 2012), but they have not addressed the role of such factors when individuals use the same habitat or target the same prey species.

Humpback whales use different feeding methods depending on the prey species. They use basic lunge feeding to capture slower-moving krill species (Ware, Friedlaender, and Nowacek 2011; Goldbogen et al. 2008; Tyson et al. 2012) and faster fish species, like anchovies and herring (Cade et al. 2020; Jurasz and Jurasz 1979). Humpbacks also use bubble-feeding to capture carangiform fish (herring) (Sharpe 2001) as well as anguilliform fish (sand lance) (Hain et al. 1982; Wiley et al. 2011). In addition to basic lunge feeding and bubble-feeding, humpback whales in the Gulf of Maine (GOM, North Atlantic

Ocean) use two additional feeding methods, bottom-feeding and kick-feeding, to target one prey species, sand lance (Hain et al. 1995; Wiley et al. 2011; Ware et al. 2014; Hain et al. 1982). Since humpback whales in the GOM use multiple feeding methods to target the same prey species, this population provides an opportunity to study how demographics and life-history state influence feeding behavior in a marine fission-fusion society unconstrained by relatedness.

The GOM humpback whale population is one of the few in which it is possible to study the influence of demographics on feeding behavior in a marine mammal species thanks to decades of multi-faceted research that has taken place in this region. In Chapter 1 of this thesis, I used long-term population data and bio-logger data from the GOM humpback whale population to explore the influence of demographics on feeding methods and the percentage of time spent feeding in a marine fission-fusion society. I tested two hypotheses: 1) The age, sex, and reproductive state of humpback whales influence their feeding methods in the GOM and 2) The age, sex, and reproductive state of humpback whales influence the percentage of time individuals spend feeding in the GOM.

In addition to studying the influence of demographics on feeding behavior, the subject of coordinated and cooperative behavior is also important to address within humpback whale fission-fusion populations. The lack of kin-based or stable, long-term associations in humpback whale fission-fusion societies should negate the need for individuals to cooperate. Nonetheless, past studies have documented cooperative behavior in SE Alaska (Sharpe 2001) and coordinated

feeding in Antarctica and the GOM (Ware et al. 2014; Wiley et al. 2011; Mastick 2016).

Long-term stable feeding groups do not occur in the GOM population, providing an opportunity to understand the cooperative dynamics of group feeding by exploring direct reciprocity through kick-feeding dyads. Kick-feeding dyads involve a pair of whales that coordinate their movements to feed together; however, researchers have yet to classify it as a form of cooperation, competition, or just a function of the prey's location and abundance. In Chapter 2 of this thesis, I used surface observations to evaluate instances of direct reciprocity and repeated events of kick-feeding dyads within and among years. I tested the hypothesis that pairs of feeding humpback whales shared the physical exertion, so their coordinated behavior was mutually beneficial, i.e., cooperative behavior. Surface observations combined with long-term life-history data provided a method to assess if kick-feeding was a form of cooperation or if demographics influenced individuals' roles in kick-feeding dyads, impeding the ability to share the physical exertion.

Chapter 1

Background

In both terrestrial and marine species, differential foraging requirements can manifest as variations in habitat use, feeding behaviors, and targeted primary prey species (Bercovitch and Berry 2017; Heide-Jørgensen et al. 2010; Cosens and Blouw 2003; Jeglinski et al. 2012; Carle et al. 2015; Welcker et al. 2009; Ruckstuhl and Neuhaus 2002). However, to sustain long-term stable groups within a population, animals are required to be at the same place at the same time and to partake in the same behavioral state (i.e., feeding, resting, or traveling) (Conradt and Roper 2000). Synchronizing time budgets within a group can be costly for individuals with differing foraging abilities (Jeglinski et al. 2012) or needs (Main, Weckerly, and Bleich 1996; Ruckstuhl and Neuhaus 2000; Conradt and Roper 2000; Lockyer 2007).

A variety of factors cause foraging needs and abilities to vary with demographics such as age, sex, or reproductive class. Often, juvenile animals have behavioral, morphological, and physiological constraints, preventing them from effectively occupying the same niche as adults (Jeglinski et al. 2012; Bercovitch and Berry 2017). Even in monomorphic species, juveniles can become segregated due to their lack of knowledge of preferred productive foraging areas (exploration-refinement foraging hypothesis) (Votier et al. 2017; Fayet et al. 2015) or less well-developed foraging skills (Fayet et al. 2015). In other species, males' and females' foraging behavior differ, and females can

target different prey trophic levels depending on their reproductive state (Carle et al. 2015).

In long-term, stable matrilineal groups the burden can fall on group members to ensure that the foraging requirements of all demographics are met, increasing the fitness of the overall genetically related group while maintaining the social structure (Tennessen et al. 2019). However, demographic segregation may also result when individuals with similar foraging needs or abilities target the same prey species or habitats (Heide-Jørgensen et al. 2010; Bercovitch and Berry 2017; Cosens and Blouw 2003; Jeglinski et al. 2012). In fission-fusion social structures, individuals do not need to conform to a social structure in which their demographic or relatedness dictates their behavioral state or associations, and they can place their own needs first.

In a fission-fusion society, groups of unrelated individuals join and split over relatively short periods (Conradt and Roper 2000), thereby negating the need for individuals to synchronize their time budgets. Studies of fission-fusion societies provide a framework in which to compare the feeding abilities and time spent feeding across demographics unrestrained by stable associations. Many studies have addressed demographic foraging differences in terrestrial and marine species; however, the ability to determine foraging differences in a population that targets the same prey species within the same marine habitat is rare.

Although many well-studied marine mammal species have long-term, stable matrilineal social structures, the humpback whale, *Megaptera novaeangliae,* is a

species with a fission-fusion society. Humpback whales have a fission-fusion social structure with most associations among individual humpback whales being short-lived (Whitehead 1983; Sardi, Weinrich, and Connor 2005; Clapham 1993; Ramp et al. 2010a; Weinrich 1991). The longest continuous association occurs between a mother and calf pair, typically lasting less than a year (Baker et al. 1990; Clapham et al. 1993; Baraff and Weinrich 1993). Due to maternally-driven site fidelity, individuals (males and females) share the same feeding ground with their maternal relatives (Katona and Beard 1990; Baker et al. 1990; Clapham et al. 1993; Palsbøll et al. 1995), but most associations do not involve first-order kin (Clapham 1993).

On the feeding grounds, humpback whales exhibit feeding strategies specific to the habitat and primary prey species (Goldbogen et al. 2015; Wiley et al. 2011; Simon, Johnson, and Madsen 2012; Ware, Friedlaender, and Nowacek 2011; McMillan, Towers, and Hildering 2018). For example, the distribution of prey in the water column has been shown to influence the probability of feeding and the method used (Hazen et al. 2009; Friedlaender et al. 2009). To capture prey, humpback whales use several different feeding methods; however, it is unknown if different demographics use different feeding methods to target the same prey species. There is previous evidence to suggest that age-class affects the way individual humpback whales interact with each other. For example, researchers found that juvenile humpback whales (1-4 years old) were more likely to be seen by themselves than adults (at least five years old), regardless of behavioral state

(Clapham 1994). Additionally, past research found that juveniles were less likely than adults to be seen in areas where the prey was closer to the surface (presumed to allow higher foraging efficiency) (Weinrich et al. 1997). In the latter study, the authors hypothesized that juveniles might have been excluded from coordinated feeding groups or outcompeted by older, more skilled individuals. The mechanics and development of feeding strategies are not fully understood. However, it may take a few years for individuals to learn a behavior (Allen et al. 2013; Weinrich, Schilling, and Belt 1992) and how to apply it across a range of conditions to consistently capture prey successfully. Therefore, an older whale may have a more extensive repertoire of feeding methods than a younger, less skilled individual.

Among adults, male and female feeding abilities may be similar; however, the amount of time spent feeding may vary based on feeding needs associated with reproductive state (Irvine et al. 2017). Most humpback whale populations migrate annually to winter breeding grounds in non-productive tropical waters (Clapham and Mayo 1987; Chittleborough 1958). The timing of humpback whale migration and the duration of time spent on the breeding grounds varies between demographics (Robbins 2007; Stevick et al. 2003; Craig et al. 2003). The total energetic cost of the time spent on breeding grounds is unknown for each demographic; however, some females have the additional energetic cost of pregnancy or lactation during the feeding season. Therefore, pregnant and lactating females may dedicate more time to feeding than other demographics,

especially when they first arrive back on the feeding grounds. Additionally, a dependent calf's needs may influence a lactating female's feeding behavior (Tyson et al. 2012; Tackaberry et al. 2020).

Although humpback whales are a well-studied species compared to many cetacean species, populations for which we have extensive knowledge of individual life-history data are uncommon. Much of what is known about the social structure of humpback whales comes from the detailed knowledge of demographic and life-history data gained during decades of data collection on North Atlantic humpback whales in the Gulf of Maine (GOM). The GOM feeding ground in the western North Atlantic ranges from Massachusetts, US to Nova Scotia, Canada. Sand lance (*Ammodytes* spp) are found throughout the southern GOM but concentrate in areas with a sandy substrate, such as Stellwagen Bank and the Great South Channel. Previous research has shown that humpback whales of all life-history stages occur in these areas and feed on sand lance.

Due to the high observational effort in the GOM, researchers can study many individuals from their calf year throughout their lives using natural markings. Studying individuals based on natural markings provides multiple opportunities to assign demographic traits and to accumulate data on life history and behavior. Long-term research in the GOM provides a basis for investigating how individuals of different sexes and age-classes feed in the same habitat.

Individual demographic and life-history data, combined with focal-follow data, provide information about the surface feeding methods used by different

demographics. Until recently, the observations were only possible during daylight hours, and subsurface behaviors went undocumented. However, the long-term tagging in the Southern GOM has significantly improved our understanding of humpback whale feeding behavior (Goldbogen et al. 2012; Ware et al. 2006; 2014; Hazen et al. 2009; Friedlaender et al. 2009). Bio-logging tags have not only provided a means to describe subsurface feeding maneuvers based on accelerometry data but certain bio-loggers, such as Customized Animal Tracking Solutions (CATS) tags, also record video (Goldbogen et al. 2017). Bio-logger video provides the ability to confirm feeding events, bubbles, and prey type. Additionally, bio-loggers can stay on a whale for over 48 hours, documenting transitions between behavioral states and feeding events when visual observations are impossible (Tackaberry et al. 2020).

By combining bio-logger data with long-term population data, I compared the feeding methods and time spent feeding between demographics. I tested the hypothesis that the age-class, sex, and reproductive state of humpback whales influence their feeding methods in the GOM. I also tested the hypothesis that age-class, sex, and reproductive state influence the percentage of time humpback whales spend feeding in the GOM. I predicted that juveniles use fewer, less elaborate feeding methods (i.e., basic lunge feeding) and spend less time feeding than adults. I expected adult males and adult females to use the same feeding methods, but that a female's feeding method would be influenced

by her reproductive state. I also predicted that lactating and pregnant females would spend more time feeding than juvenile or nulliparous females.

Methods

Archival tag dataset

I used bio-logger data from the Stellwagen Bank National Marine Sanctuary (SBNMS) yearly tagging project collected during the 2015-2019 feeding seasons. SBNMS worked with multiple academic, governmental, and non-profit organizations for two weeks per year in mid to late June from 2004-2019 to study humpback whales' feeding behavior using bio-loggers. In 2015, SBNMS started deploying CATS (Custom Animal Tracking Solutions) tags. The CATS tags were attached using non-invasive suction cups and included 3-axis accelerometers, magnetometers, pressure sensors, gyroscopes, and 1 or 2 video cameras (Cade et al. 2016; Goldbogen et al. 2017).

Most of the tagging effort occurred off the coast of southern Massachusetts, from the Stellwagen Bank National Marine Sanctuary to the waters east of Cape Cod, Massachusetts (Figure 1). Tagging occurred between June 12 and June 26 annually from 2015-2019. The research teams tended to deploy tags in the area closest to the port of departure with a large aggregation of foraging whales. The teams also typically favored whales surface feeding with associates and other behaviors that facilitated tag deployment (such as extended time at the surface). Similar methods and protocols were used every year, as described by Friedlaender et al. (2009) and Wiley et al. (2011). For this study, I excluded

deployments that did not have accurate accelerometry data, deployments in which the video did not record, or deployments during which the tag remained on the whale for less than thirty minutes.

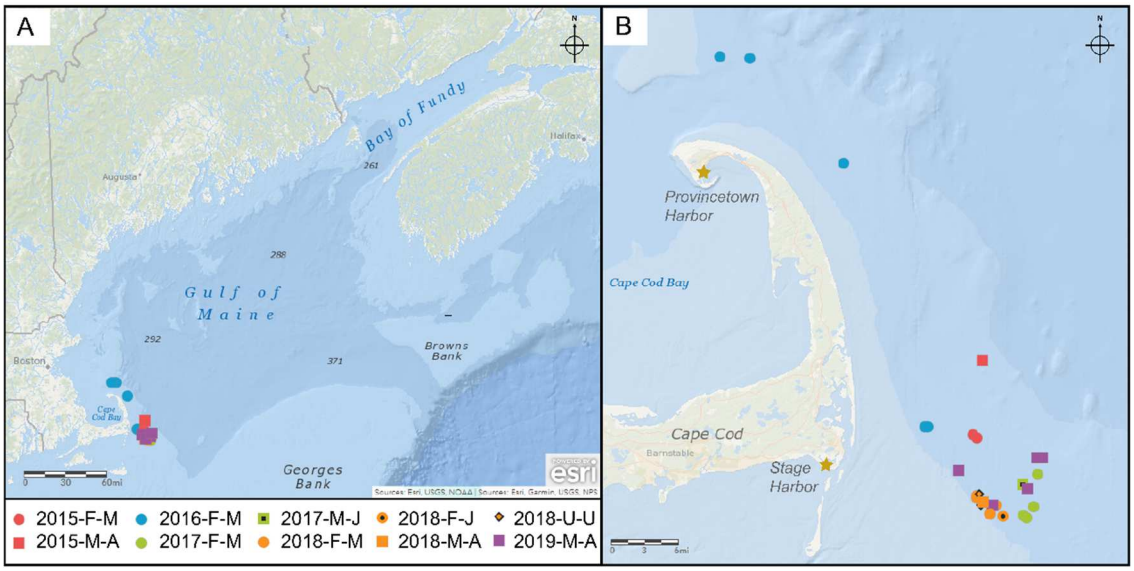

Figure 1. Map of the bio-logger deployments on humpback whales in the Southern Gulf of Maine within the North Atlantic. A) A map of the Gulf of Maine (GOM) in the western North Atlantic. All of the tagging occurred in the Southern GOM where sand lance is the primary prey species. B) A closer view of the tag deployment locations around Cape Cod. Most tag deployments occurred in the region where a large aggregation of foraging whales was found closest to the port of departure (either Provincetown or Stage Harbor).

Once a tag was deployed, a team initiated a “focal-follow” in which researchers recorded the surface behavior and location of the tagged whales and their associates (Altmann 1974). The focal-follow team used an 80-code behavioral ethogram developed by the Whale Center of New England (WCNE) to characterize the surface behaviors of tagged whales and their associates. Focal-follows continued until the tag fell off, weather or darkness made conditions unproductive or unsafe to continue, or the team was needed to collect data from

another tagged whale. The duration of focal-follows ranged from 15 minutes to over seven hours. When available, I used the focal-follow data to confirm kick-feeding events, the behavior of individuals associated with the tagged whale, and the presence of bubbles at the surface.

Pseudotrack data

TrackPlot (Ware et al. 2006) was used to create three-dimensional pseudotracks to facilitate the identification of feeding methods during tag deployments. The pseudotrack included a "ribbon" representing the whale's track that displayed the whale's orientation (pitch, yaw, roll), fluke stroke, depth, and estimated speed (Ware et al. 2006). An animated humpback whale model moved along the pseudotrack as I replayed the deployment. For each deployment, I imported a video of the TrackPlot pseudotrack into Behavioral Observation Research Interactive Software (BORIS) (Friard and Gamba 2016). Within BORIS, I developed a custom ethogram to characterize the behaviors suggested by the tag data. I visually audited the pseudotrack for feeding events and behavioral states. Behavioral states were marked for the behavior's duration while feeding events were marked as an occurrence, not the duration, of a feeding event/lunge. I noted feeding events at the start of each feeding method, such as at the start of a spiral, kick at the surface, or roll at the bottom of a dive.

Feeding methods/Behavioral states

This study focused on four previously described feeding methods: bubble-feeding (bubble-net and bubble clouds), bottom-feeding, kick-feeding (originally

termed 'inside loop,' also known as 'double-loop' and lobtail feeding), and basic lunge feeding (Hain et al. 1982; 1995; Wiley et al. 2011; Ware et al. 2014; Allen et al. 2013; Weinrich, Schilling, and Belt 1992; Weinrich et al. 1997; Johnson and Tyack 2003). However, each whale used a slightly different series of actions/movements within these feeding methods. For example, the size and formation of bubbles used to corral fish varied from a series of small, effervescent bubbles released in a large ring to one or more large bubbles that formed a dense ring or cloud (Hain et al. 1982). Kick-feeding included individualistic sequences of movements, such as the specific number of times a whale slapped the water surface with its tail and the timing or strength of each kick (Wiley et al. 2011; Weinrich, Schilling, and Belt 1992).

The feeding events were categorized as follows: bottom-feeding (Ware et al. 2014), bubble-feeding (Wiley et al. 2011), kick-feeding (Wiley et al. 2011), basic lunge feeding (Wiley et al. 2011), or other/previously undescribed. Feeding events were confirmed using video collected from the CATS tag when it documented the presence of bubbles, prey, an open gape, or a view of associated whales engaged in feeding. However, the act of slapping the surface of the water during kick-feeding was not always visually captured by the CATS tag since most of the deployments were placed anterior to the dorsal fin and had a forward-facing orientation. Therefore, when the pseudotrack and the posture of the whale’s body in the camera’s view resembled kick-feeding, I referred to focal-

follow data to confirm that the unique sequence of behaviors represented kick-feeding for that individual.

Feeding, surface active, and non-feeding/other behavioral states were assigned based on feeding events and time between the feeding events. If the time between feeding events was less than 20 minutes, the whale was assumed to have remained in a feeding behavioral state since it may have been searching for another viable prey patch before feeding again. I selected 20 minutes to be conservative before transitioning away from feeding. In other populations, foraging dives have not exceeded 10 minutes (Goldbogen et al. 2008), and 20 minutes would allow for a whale to remain in a feeding behavioral state with two failed foraging dives before successfully feeding again. If the time between feeding events was greater than 20 minutes, the whale was assumed to no longer be feeding and re-categorized to a non-feeding/other behavioral state. The transition between feeding and non-feeding behavioral states occurred at the beginning of the first dive after the last feeding event. The non-feeding behavioral state encompassed any time not spent either feeding or in a surface-active behavioral state. The speed, dive depth, and distance that an animal covered was not considered. The transition back to a feeding behavioral state was noted just before the first feeding event.

Long-term population dataset

I used demographic data from long-term studies of humpback whales conducted by the Center for Coastal Studies (CCS). CCS has studied humpback

whales in the GOM since 1976, including through annual boat-based surveys spanning the GOM feeding range since 1989. CCS researchers photograph the ventral flukes and dorsal fins of whales to identify individuals (Katona and Whitehead 1981) and collect genetic samples to sex individuals (Bérubé and Palsbøll 1996b; 1996a; Palsbøll et al. 1992). Alternative sexing methods include photos of genital slits and calving history (Glockner 1983). Researchers record the identity of mother-calf pairs to track individuals throughout their lives and document maternal lineages.

Using life-history data from the CCS Gulf of Maine Humpback Whale Catalog, I assigned sex and age-class to tagged individuals. I classified whales as male, female, or unknown sex based on genetics, photos, or sightings history data. Based on their sighting history, I also classified whales as adult, juvenile, or unknown age-class. Age-class was assigned with certainty to individuals with a known year of birth. Adults were at least five years old (Robbins 2007; Clapham 1992), and whales that were one to four years old were considered juveniles (Robbins 2007; Clapham 1992). I assigned age-class to a portion of whales of unknown ages who were first documented after their calf year. A sighting history length of at least four years ensured the whale was at least five years old when it was tagged, therefore classified as an adult. Whales that were not seen while a calf but had a sighting history of fewer than four years were classified as unknown since I could not determine if they were juveniles or previously undocumented older individuals.

For this analysis, I used the sighting history and presence of a dependent calf to assign reproductive states to the females. Adult females (at least five years old) were categorized as nulliparous, parous, pregnant, or lactating. The nulliparous classification included females that had reached the minimum age of first calving and never been seen with a calf but could have been pregnant or had a calf that was unobserved. The category parous included sexually mature females that had given birth previously but did not have a dependent calf the year after they were tagged or were not seen by researchers during the year post tagging to confirm if they had a dependent calf. Therefore, the parous classification includes both resting females (not pregnant) and females that could not be confirmed as pregnant. Females were retroactively classified as pregnant if they were documented with a calf the year after they were tagged. The lactating category included tagged females with a dependent calf. Gestation nearly one year (~11.5 months) (Clapham and Mayo 1987; Chittleborough 1958; Baker, Perry, and Herman 1987; Oftedal 1997) followed by an extended period of nursing until weaning occurs in the fall or winter (Baraff and Weinrich 1993). Therefore, since the tagging effort occurred from mid to late June, females were in the first half of their pregnancy, and lactating females had been nursing their calves for approximately 3-6 months.

Analysis

The first goal of this study was to determine the influence of sex, age-class, and reproductive states on feeding methods used by tagged whales. To

determine if the use of feeding methods among demographics differed from expected values based on random chance, I used Chi-square test of independence with a Bonferroni correction. However, some sample sizes were small; therefore, when the expected cell value was less than five, I used a two-sided Fisher's exact test with a Bonferroni correction. The tag deployments varied in duration and were not evenly distributed among the different demographics. To determine if the tag deployment's length was a confounding factor for the number of feeding methods detected per deployment, I used linear regression. Analysis of variance (ANOVA) was used to determine the influence of sex, age-class, and reproductive state on the number of feeding methods used.

The second goal was to determine the influence of sex, age, and reproductive state on the percentage of tagged time the individual spent feeding. Since the sample sizes were small for some demographics, I ran three separate one-way ANOVAs to determine the influence of sex, age, and reproductive state on the percentage of time individuals spent feeding with a Bonferroni correction. All statistical analysis was completed in R 3.6.2 (R Core Team 2019) and RStudio (RStudio Team 2019).

Results

In total, 29 CATS tag deployments between 2015 and 2019 met the inclusion criteria in this study (Table 1). All but one of the deployments involved whales successfully matched to the CCS Gulf of Maine Humpback Whale Catalog.

Table1. Tag Deployments

Tag_ID	Sex, age-class, and reproductive state	Behavioral coding duration (hours)	Percentage of time spent feeding	Number of feeding methods	Bottom-feeding	Bubble-feeding	Kick-feeding	Confirmed lunge feeding, no disturbance	Confirmed lunge feeding, disturbance	Unconfirmed lunge feeding	Other feeding method
20150618-A	M-Ad	7.5	70	1	No	Yes	No	No	No	No	No
20150622-B	F-Pr	5.7	66	2	No	Yes	Yes	No	No	No	No
20150622-C	F-Pr	13.7	91	2	No	Yes	No	No	No	Yes	No
20160615-A	F-Pa	34.5	40	3	Yes	No	Yes	No	No	Yes	No
20160615-B	F-Pa	3.2	12	1	Yes	No	No	No	No	No	No
20160617-C	F-La	3.7	91	3	Yes	Yes	Yes	No	No	No	No
20160619-D	F-Pr	19.5	30	3	Yes	Yes	Yes	No	No	No	No
20160622-E	F-La	26.8	50	3	Yes	Yes	No	No	Yes	No	No
20170612-A	M-Ju	0.7	100	1	No	Yes	No	No	No	No	No
20170612-B	F-Pa	23.1	56	4	Yes	Yes	Yes	No	Yes	No	No
20170613-C	F-La	2.2	100	1	Yes	No	No	No	No	No	No
20170615-D	F-Pa	1.1	67	1	Yes	No	No	No	No	No	No
20170615-E	F-Pa	26.9	78	3	Yes	Yes	No	No	Yes	No	No
20180620-A	F-Ju	10.7	40	2	Yes	Yes	No	No	No	No	No
20180620-B	F-Nu	27.8	68	1	Yes	No	No	No	No	No	No
20180620-C	F-Ju	4.7	26	1	Yes	No	No	No	No	No	No
20180621-D	F-Nu	12.2	41	1	Yes	No	No	No	No	No	No
20180622-E	U-Un	2.9	100	1	Yes	No	No	No	No	No	No
20180622-F	F-Pa	1.0	100	1	Yes	No	No	No	No	No	No
20180624-G	F-Pa	1.0	43	2	No	Yes	No	No	Yes	No	No
20180624-H	F-Pa	10.9	11	2	Yes	Yes	No	No	No	No	No
20180624-I	U-Un	18.4	69	1	Yes	No	No	No	No	No	No
20180624-J	U-Ad	1.3	3	1	Yes	No	No	No	No	No	No
20180626-K	M-Ad	7.9	0	0	No	No	No	No	No	No	No
20190618-A	M-Ad	52.1	53	4	No	Yes	Yes	No	No	Yes	Yes
20190618-B	M-Ad	39.5	79	3	No	Yes	Yes	No	Yes	Yes	No
20190619-C	M-Ad	0.9	100	2	No	Yes	No	Yes	No	Yes	No
20190623-D	M-Ad	1.5	100	1	No	No	No	No	No	Yes	No
20190624-E	M-Ad	33.8	52	4	Yes	Yes	Yes	No	No	Yes	No

Note: M: male, F: female, U: unknown sex, Ad: adult, Ju: juvenile, Un: unknown age-class, Nu: nulliparous, Pa: parous, Pr: pregnant, La: lactating.

One individual did not have adequate photo-identification data to match to a previously cataloged individual. I still included this whale in the study since it was not a dependent calf, and it was not the only tagged whale of unknown sex or age-class. Sixty-two percent of the tagged whales were female (n = 18), 28% were male (n = 8), and the sex of 10% of the whales (n = 3) was not known (Table 1). The majority of tagged whales were adults (83%, n = 24), with only 10% classified as juveniles (n = 3) and 7% of unknown age-class (n = 2). Within the adult female deployments, 50% of the females were parous (n = 8), the same percentage of females were lactating (19%, n = 3) or pregnant (19%, n = 3), with fewer nulliparous females (13%, n = 2).

There was variation in deployment duration, the proportion of demographics tagged, and the geographic location of the deployments. The length of behaviorally coded deployment data ranged from 41 minutes to 52.1 hours (Table 1). The median tag duration was 7.9 hours, and the average duration was 13.6 hours. All four feeding methods were detected during the study. Bottom-feeding occurred on the majority of tag deployments (66% ±3%, n = 19), followed by bubble-feeding (55% ±3%, n = 16), kick-feeding (28% ±2%, n = 8), and basic lunge feeding (21% ±2%, n = 6). An additional feeding method occurred on a deployment that did not fall into one of the four predetermined categories. A male used slow horizontal side lunges at night within 30 m of the surface, but the prey species could not be determined. Since this feeding method was only detected on a single deployment it was excluded, and only the four main feeding methods

(bottom-feeding, bubble-feeding, kick-feeding, and basic lunge feeding) were used during the analysis of the influence of demographics on feeding methods.

Influences of demographics on feeding methods

Sex. Both males (n = 7) and females (n = 18) used the four main feeding methods (bottom-feeding, bubble-feeding, kick-feeding, and confirmed basic lunge feeding). The single deployment without any feeding behavior involved a male and was excluded from the analysis of the influence of demographics on feeding methods. Bubble feeding was the most common feeding behavior of males occurring in 71% of male deployments (n = 5). Bottom feeding was the least common, only occurring in 14% of the male deployments (n = 1). However, with the small sample size, we could not detect a difference in the frequency of these two behaviors (two-sided Fisher's exact test p = 0.072, Bonferroni adjusted p = 0.434, Figure 2). In contrast, more females used bottom-feeding and bubble-feeding than expected, and fewer females used kick-feeding or basic lunge feeding (Chi-square, $\chi^2 = 17.164$, df = 3, p = 0.001, Bonferroni adjusted p = 0.004). I completed four statistical tests to determine the difference between male and female use of bubble-feeding, bottom-feeding, kick-feeding, and confirmed basic lunges. The only significant difference was that more females and fewer males used bottom-feeding than expected by random chance (two-sided Fisher's exact test p = 0.003, Bonferroni adjusted p = 0.017).

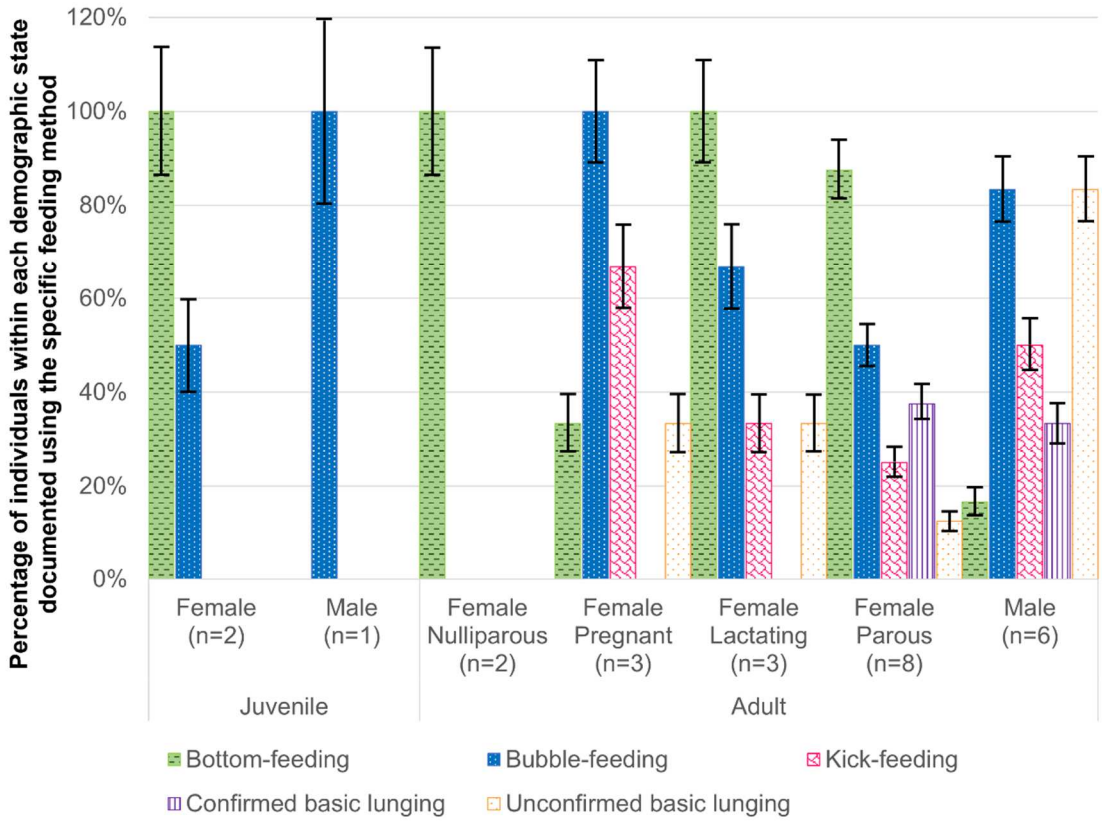

Figure 2. Percentage of individuals within each demographic state documented using bottom-feeding, bubble-feeding, kick-feeding, or lunging feeding. Adults were documented using all feeding methods while juveniles were documented only using bubble-feeding and/or bottom-feeding. Lunge feeding was split into two categories: confirmed lunges in which the tagged whale did not blow any bubbles and unconfirmed lunges in which due to camera angle or lack of video, it could not be confirmed if the tagged whale blew bubbles or not. Individuals of unknown sex and/or age (n = 3) were excluded from this figure, but all three were only documented bottom feeding.

Age-class. Adults (n = 22) used all four main feeding methods (bottom-feeding, bubble-feeding, kick-feeding, and basic lunge feeding), but juveniles (n = 3) only used bottom-feeding and bubble-feeding (Figure 2). Although juveniles did not use kick-feeding or basic lunge feeding, the sample size was too small to determine if this was significant (two-sided Fisher's exact test, p = 0.182,

Bonferroni adjusted p = 0.364). Correspondingly, more adult whales (males and females) used bottom-feeding and bubble-feeding compared to kick-feeding or basic lunge feeding (Chi-square, $\chi^2 = 10.261$, df = 3, p = 0.016, Bonferroni adjusted p = 0.033).

Reproductive state. Female reproductive state did not appear to influence feeding method; however, some sample sizes were small. Lactating, pregnant, and parous females used all four main feeding methods (Figure 2). Although bottom-feeding was the only feeding method used by nulliparous females (n = 2), the differences among the reproductive states were not statistically significant (two-sided Fisher's exact test, p = 0.853).

Confounding factors. The absence of certain feeding methods during some of the deployments may have been due to tag deployment length more than the individual's life-history state. The length of the tag deployment did influence the number of different feeding methods detected (Linear regression, adjusted R^2 = 0.486, $F_{1,27} = 27.520$, $p = 1.573 \times 10^{-5}$, Figure 3). Tag duration was not even across demographics. Two of three tag deployments on juveniles were under the median tag duration (7.9hrs), and all of the juvenile deployments were under the average duration of 13.6hrs. Therefore, the shorter deployments on juveniles may have restricted the opportunity to capture additional feeding methods.

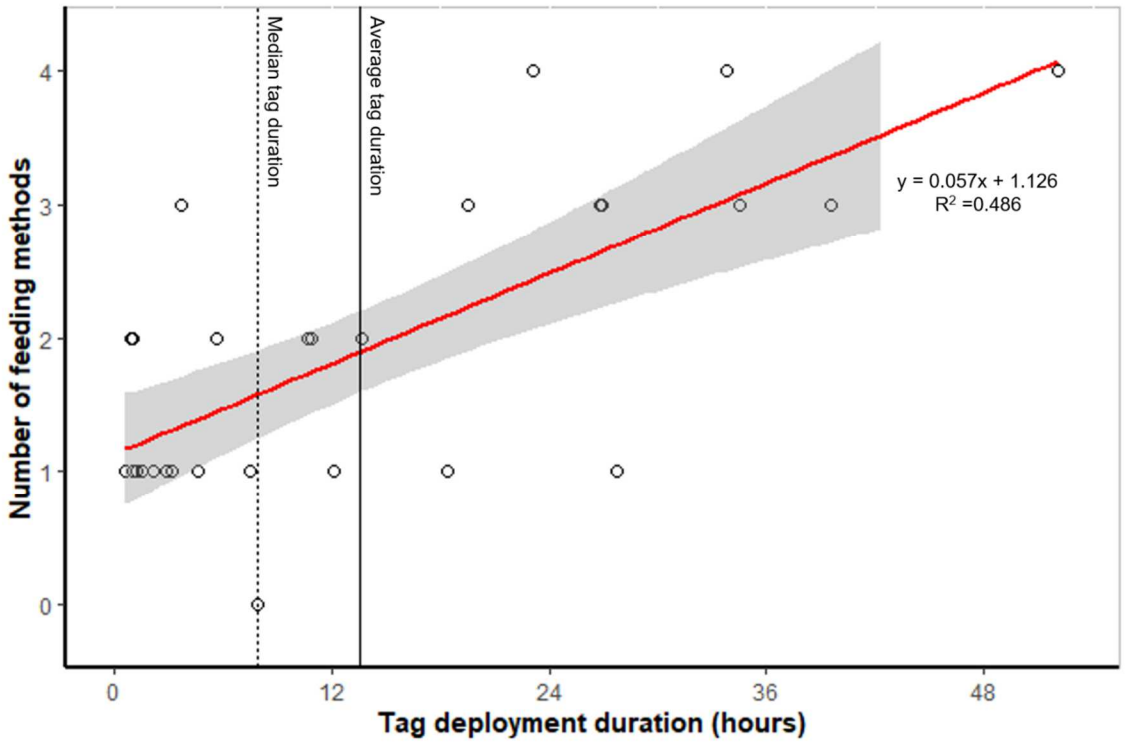

Figure 3. **The number of feeding methods documented during each tag deployment compared to the duration of the deployment.** The number of different feeding methods detected during a tag deployment differs with the length of the tag deployment **(**Linear regression, number of feeding methods = 1.126 + 0.057(duration), adjusted R^2 = 0.486, $F_{1,27}$ = 27.520, p = 1.573×10^{-5}). I was less likely to document three or four feeding methods during a deployment when it was shorter than the average or median value.

Behavioral States/Time budget

Feeding occurred on all but one tag deployment. When feeding was detected, the percentage of time spent in a feeding behavioral state ranged from 3%-100% of the total tag duration. When comparing individual tag deployments, age-class, sex, and reproductive state did not influence the percentage of time an individual spent feeding (juvenile-adult: ANOVA, $F_{1,25}$ = 0.024, p = 0.879, Bonferroni adjusted p = 1; male-female: ANOVA, $F_{1,24}$ = 1.035, p = 0.319, Bonferroni

adjusted p = 1; adult male-adult female: ANOVA, $F_{1,21}$ = 1.174, p = 0.681, Bonferroni adjusted p =1; female reproductive state: ANOVA, $F_{4,13}$ = 0.978, p = 0.453, Bonferroni adjusted p = 1; Figure 4). The sample sizes were too small to compare between age classes of different sexes; therefore, despite the apparent differences between juvenile males and juvenile females, the single juvenile male with a high percentage of time spent feeding could be an outlier and not typical of that demographic Among females, the percentage of time spent feeding did overlap between different demographics. Although not significant, the results suggest that lactating females may spend more time feeding, and juveniles possibly spend less time feeding than other females (Figure 4).

One female was tagged during consecutive years, allowing for a comparison of behaviors in two reproductive states. The female was tagged while pregnant in 2015 and while lactating in 2016. Although her deployment was shorter in 2016 (3.7hrs compared to 5.7hrs), she spent 91% of her time in a feeding state when she had a calf compared with only 66% of her time while pregnant.

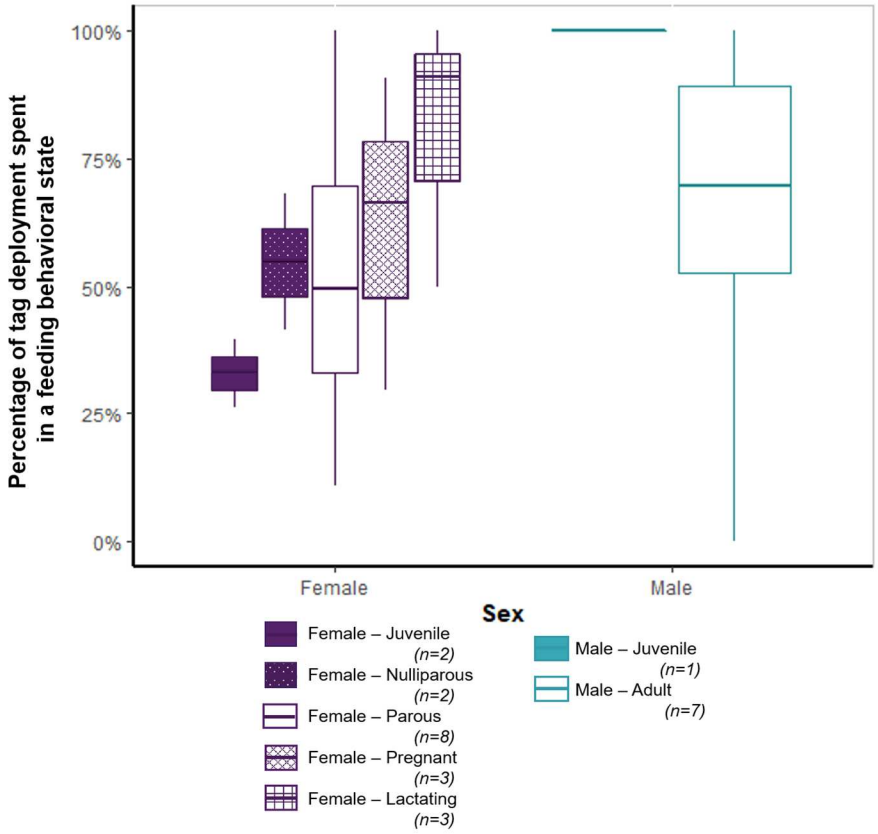

Figure 4. Comparison of demographics to the percentage of time spent in a foraging behavioral state during tag deployments. Age-class, sex, and reproductive state did not influence the percentage of time an individual spent feeding (juvenile-adult: ANOVA, $F_{1,25} = 0.024$, $p = 0.879$, Bonferroni adjusted $p = 1$; male-female: ANOVA, $F_{1,24} = 1.035$, $p = 0.319$, Bonferroni adjusted $p = 0.958$; female reproductive state: ANOVA, $F_{4,13} = 0.978$, $p = 0.453$, Bonferroni adjusted $p = 1$).

Discussion

Influences of demographics on feeding methods

Sex. The results supported my expectation that sex did not influence the number of feeding methods used by males and females. Sex also did not influence the use of kick-feeding, which is in agreement with previous studies (Weinrich, Schilling, and Belt 1992; Allen et al. 2013). Additionally, there was no

difference detected between males and females regarding bubble-feeding or lunge feeding; however, females used bottom-feeding more often than males. Further data are needed to differentiate individual preferences from the environmental factors that dictate the percentage of time sand lance spend close to the substrate (which would force bottom feeding over other feeding methods). Increased tagging effort at different times of the feeding season could provide information about changes in prey behavior and how that relates to the use of different feeding methods.

Age-class. The data supported the prediction that juveniles would use fewer feeding methods than adults. However, the prediction that juveniles would use less complex feeding methods, like basic lunge feeding, was not supported. Basic lunge feeding was one of the least documented feeding methods in the study; however, no one- or two-year-olds were tagged. Therefore, these results do not exclude basic lunge feeding within the first year or two of independence.

Like basic lunge feeding, kick-feeding did not occur during juvenile deployments. The lack of kick-feeding in juvenile tag deployments is likely due to a combination of a few factors and is consistent with expectations based on the results of previous research. Allen et al. (2013) and Weinrich et al. (Weinrich, Schilling, and Belt 1992) found that fewer than 2% of kick-feeders were less than two years old and hypothesized that it took an individual a few years to learn and perfect this feeding method. Juveniles also encompassed only 10% of the tagged whales, reflecting the lower overall frequency of juveniles in the GOM population

(Robbins 2007). Regardless of demographic, basic lunge feeding and kick-feeding were used by fewer tagged whales, occurring in only 21% (±2%) and 28% (±2%) of tag deployments compared to bottom-feeding (66% (±3%)) and bubble-feeding (55% (±3%)). Therefore, the probability of documenting a less frequent behavior could have been exacerbated by the shorter tag deployments on juveniles, which was statistically shown to reduce the number of feeding methods detected. A higher level of tagging effort targeting juveniles or analysis of long-term sightings data would provide the larger sample size needed to determine the usage of basic lunge feeding or kick-feeding in this age-class.

Reproductive state. These results suggest that reproductive state does not influence the type of feeding method used by tagged individuals. Excluding nulliparous females, adult females used all four main feeding methods regardless of their reproductive state. Although nulliparous females only used bottom-feeding, the lack of additional feeding methods was not a result of short tag durations (the nulliparous tag deployments were 12.2hrs and 27.8hrs). There is not an apparent reason why nulliparous females would have only used bottom-feeding during the study, but sample size was only two individuals. A larger sample size would provide a better understanding of the feeding methods used by this demographic. However, regardless of their reproductive state, the use of bottom-feeding by almost every female in this study suggests it is a critical feeding method for females.

Pregnant females and lactating females with their dependent calves must travel through the entire depth of the water column to bottom-feed, which puts them at a higher risk for anthropogenic threats throughout the water column, including fishing gear and line along the substrate. The heavy use of the lower water column by females should be taken into consideration in future studies of anthropogenic impacts, which tend to concentrate on the surface threats (Calambokidis et al. 2019; Baumgartner and Mate 2003; Robbins and Tackaberry 2011; Cassoff et al. 2011).

Behavioral States/Time budget

The influence of age, sex, and reproductive state on the percentage of time spent feeding was not statistically significant. However, the data suggested females in this study might spend a higher percentage of their time feeding when lactating than when in other reproductive states. Although this trend may suggest differences within females, the tagging effort occurred in mid-June, soon after lactating females returned from the feeding ground compared to pregnant females who returned as early as March (Robbins 2007). Female feeding requirements likely change throughout the feeding season depending on the duration of their residency on the feeding grounds and the progress in their pregnancy or weaning of their calf (Tyson et al. 2012). Additional tagging effort throughout the feeding season will help detect changes in female feeding requirements across the feeding season.

It is likely that longer deployments will provide more data on the overall amount of time different demographics spend feeding and how that varies across multiple days and environmental conditions. Unfortunately, the technology does not currently allow multi-day deployments on humpback whales with the ability to record video for the entirety of the tag deployment. However, once the accelerometry signals of all GOM feeding methods are described and verified with video, that information can be applied to mid- or long-term duration bio-loggers without video capabilities.

There are likely more factors than just an individual's life-history state that influence the amount of time whales spend feeding. An individual's overall health, body size, and behavior before being tagged (possibly feeding or not for multiple hours beforehand) could influence the amount of time an individual spends feeding during the tag deployment. Additionally, environmental conditions and the amount of prey available also influence an individual's behavior (Hazen et al. 2009). This study focuses on data from the late spring after whales return from the breeding ground and before the peak of the summer feeding season. A better understanding of how the feeding activities of different demographics change throughout the feeding season could be accomplished by replicating this study with early, peak, and late-season tag deployments.

Conclusion

Long-term, multi-faceted humpback whale research has provided a window into the influence of age, sex, and reproductive state on feeding behavior within a

fission-fusion society. This analysis examined the influence of demographic class of individuals feeding within the same habitat and prey type while excluding confounding factors such as relatedness or demographic segregation.

The results suggest that the sex of an individual influenced some of the feeding method that it used in the GOM. Adults had an extensive repertoire of feeding methods they could use, but some feeding methods were more prevalent than others (bottom-feeding and bubble-feeding). As predicted, juveniles did not appear to have as large a repertoire as adults. However, the failure to detect all feeding methods in juveniles was likely caused by a combination of a small sample size, shorter tag deployment lengths, and lack of experience/skill. Although there was no substantial evidence that the percentage of time spent feeding was influenced by demographics, the trend that lactating females may spend a higher percentage of their time feeding highlights the need to study how energetic requirements change throughout the feeding season. These changes are particularly important to determine in females as nursing rates may decrease throughout the weaning process, and females' foraging needs may change as their pregnancy progresses.

This study demonstrates the benefit of studying foraging dynamics at the individual level using demographic and life-history data. Long-term population data from a fission-fusion society combined with bio-loggers provided insight into the percentage of time spent feeding and the feeding methods used by different demographics while targeted the same prey species. Not only does this study set

the stage for future research on the energetic benefits of different feeding methods, but it also highlights the need to incorporate information about the behaviors of different demographics while assessing anthropogenic threats to the overall population.

Chapter 2

Background

Many species use coordinated and cooperative behaviors, including species with fission-fusion social structures (Bercovitch and Berry 2013). A fission-fusion social structure involves individuals that are not closely related joining and splitting over relatively short periods and is a widespread social structure in many species (i.e., African buffalo (*Syncerus caffe*r) (Cross, Lloyd-Smith, and Getz 2005), spotted hyena (*Crocuta crocuta)* (Smith, Memenis, and Holekamp 2007), big brown bats (*Eptesicus fuscus*) (Metheny et al. 2008), and Grevy's zebra (*Equus grevyi)* and onager (*Equus hemionus khur)* (Sundaresan et al. 2007). The absence of stable, long-term associations and lack of kinship between group members brings into question the motivation behind cooperative behavior when it occurs. Past studies on cooperative behavior in fission-fusion societies focused on the influence of ecological factors, such as food availability and predator avoidance (Bercovitch and Berry 2013; Sundaresan et al. 2007). However, non-ecological factors, such as age, sex, and reproductive state, can also influence social dynamics.

In simple terms, cooperation is when individuals work together to obtain a mutual goal (Boesch and Boesch 1989). However, in the field of social evolution, cooperation is more complex (West, Griffin, and Gardner 2007). Cooperation is a behavior evolutionarily selected for because of the benefits gained by an individual (termed receiver) due to another individual's acts (termed actor) (West,

Griffin, and Gardner 2007). By this definition, cooperative behavior may either decrease (-) or increase (+) the actor's *direct* fitness (individual reproductive success) (West, Griffin, and Gardner 2007). Therefore, cooperation includes altruism and mutually beneficial behaviors, reserving the term mutualism for inter-species interactions (West, Griffin, and Gardner 2007; Hamilton 1964a). A behavior is mutually beneficial when the actor and receiver increase their direct fitness, even if the actor does not gain as much benefit as the receiver. This situation is known as weak altruism (West, Griffin, and Gardner 2007). Regardless of the type of cooperation, the actor and receiver's *inclusive* fitness (sum of an individual's direct and indirect fitness (reproductive success of genetic relatives)) increase during cooperative behaviors (West, Griffin, and Gardner 2007). In contrast, when an actor benefits and the receiver's inclusive fitness decreases, the behavior is categorized as a form of selfishness (+/-) (West, Griffin, and Gardner 2007; Hamilton 1970; 1964a).

Altruistic cooperation (-/+) is thought to be evolutionarily advantageous to the actor because of the indirect benefits of what appears to be a costly behavior (West, Griffin, and Gardner 2007). The actor's indirect benefit manifests as elevated indirect fitness through increased reproduction of individuals sharing a similar genetic trait (West, Griffin, and Gardner 2007; Hamilton 1964a; 1964b; Bourke 2021). Individuals with a similar genetic trait are not only individuals with common ancestry (kin discrimination or limited dispersal), but this also includes non-kin who share the same genetic trait (“greenbeard effects”) (West, Griffin,

and Gardner 2007). Altruistic cooperation does not improve the actor's direct fitness but does increase the number of individuals in the population that share a same genetic trait.

Mutually beneficial cooperation (+/+) is thought to be selected for due to the direct benefits to both the actor and receiver, which thereby increase both individuals' fitness (West, Griffin, and Gardner 2007). In mutually beneficial cooperation, the actor and receiver's relatedness is not critical since both directly benefit from the partnership. However, the direct benefit to both the actor and receiver does not necessarily occur simultaneously. Mutually beneficial cooperation may require a mechanism to ensure the receiver will repay the original cost to the actor. One of the established mechanisms is reciprocity (West, Griffin, and Gardner 2007). There are many forms of reciprocity (direct, indirect -upstream & downstream, strong, and generalized) found in cooperative behavior (West, Griffin, and Gardner 2007; Pfeiffer et al. 2005; Nowak and Roch 2007; Molesti and Majolo 2017; Whitehead 2008; Nowak and Sigmund 2005). Within direct reciprocity, two individuals share the benefits of an action through role exchange during repeated interactions. Although separately each exchange may appear to be altruistic (Brown 1983), when a pair's interactions over time are holistically reviewed, both individuals mutually benefit from the association (Nowak and Sigmund 2005; Brown 1983).

In wild populations, determining if behaviors are cooperative can be difficult. Cooperation is sometimes assumed when coordinated behaviors are

documented. Coordinated behaviors involve group members synchronizing their movements in time and space (Boesch and Boesch 1989; Bailey, Myatt, and Wilson 2013). Observations of behaviors that appear to be coordinated movements could result from prey location or density and do not necessarily imply cooperation between individuals. In comparison, collaboration is a more complex form of coordination, when individuals hunt the same prey together while performing different complementary movements, rather than the same actions (Boesch and Boesch 1989; Bailey, Myatt, and Wilson 2013). During these collaborations, individuals may bear different energetic costs depending on their role in the foraging group (Sharpe 2001). It is difficult to determine if a collaborative behavior is a form of cooperation, especially if the long-term effects on individual fitness (indirect benefits) are hard to track and separate from other behaviors or environmental conditions individuals are experiencing. However, observations of direct reciprocity between individuals performing a collaborative behavior suggest mutually beneficial cooperation. Repeated interactions between individuals and instances of direct reciprocity can be tracked over time during long-term behavioral studies to evaluate evidence for cooperative behavior within a population.

Conducting long-term behavioral studies about cooperative behavior using direct reciprocity can be challenging in wild populations but is especially difficult in less accessible species, such as marine mammals. Most marine mammals are long-lived species that spend most of their lives beneath the ocean's surface;

therefore, the ability to record their interactions and interpret their behaviors is difficult. In particular, collaborative coordinated behaviors in which direct reciprocity can be investigated and observed from the surface are rare.

One collaborative coordinated behavior found in a marine mammal population in which direct reciprocity can be investigated is kick-feeding. Kick-feeding is a collaborative coordinated feeding method used by humpback whales, *Megaptera novaeangliae*, and represents a collaborative coordinated behavior with different cost-benefits to different group members (Hain et al. 1982). The identification of actors and receivers through surface observations provides a method to determine if direct reciprocity occurs over time. Individual demographics can also be explored to more fully understand other potential factors that may influence the composition of kick-feeding associations.

Kick-feeding is a behavior that has thus far only been described in the Gulf of Maine (GOM) in the North Atlantic. It has been hypothesized to have developed among humpback whales as a method to target sand lance (*Ammodytes* spp) after a collapse in herring stocks in the 1980s (Weinrich et al. 1997; Weinrich, Schilling, and Belt 1992; Hain et al. 1982). Kick-feeding spread through the southern GOM via cultural transmission among non-related individuals (Allen et al. 2013; Weinrich, Schilling, and Belt 1992; Weinrich et al. 1997).

During kick-feeding, one whale (the actor) will create a disturbance by striking the water's surface with its flukes, flippers, or head sometimes with the addition of releasing bubbles, and then lunge through the disturbance (Weinrich, Schilling,

and Belt 1992). No calves and very few whales under three years old have been documented using this feeding method (Allen et al. 2013; Weinrich, Schilling, and Belt 1992). In theory, this may be due to learning or a certain level of development that is required before kick-feeding can be attempted, let alone successful (Allen et al. 2013; Weinrich, Schilling, and Belt 1992).

Although whales can kick-feed by themselves, dyads form in which another whale (the receiver) also lunge feeds in the disturbance, appearing to take advantage of the kicker's actions (Hain et al. 1982). However, the receiver's contribution to corralling the prey is unknown. The results of Chapter 1 suggest that a whale lunging through another whale's bubble cloud/disturbance is rare. More often, this second individual released at least a few bubbles which may have contributed to the corralling of the prey. There may also be other undocumented contributory behaviors by the second individual, such as sound production. However, we assume the actor's energetic cost of performing the surface behavior unique to kick-feeding (which can also involve releasing bubbles) is greater than the receiver's cost, regardless of the receiver's contributions.

Although researchers have studied kick-feeding since the 1980s, they have yet to classify this collaborative coordinated feeding behavior as a form of cooperation or competition. Kick-feeding might be a form of mutually beneficial cooperation if repeated associations between individuals occur within or across years with an exchange of roles (direct reciprocity). Even if role exchange does

not occur, if a kick-feeding dyad's collaborative behavior increases the amount of prey consumed versus when directly competing with each other, those pairs should seek each other out to increase their efficiency (weak altruism).

If direct reciprocity is not evident, then one possible explanation for the lack of role exchange within kick-feeding dyads is a behavioral constraint that prevents receivers from also being actors. Ascertaining the demographic composition of dyads can provide insight into the role of age, sex, and reproductive state play in determining a whale's role within a dyad. For example, in other species, younger individuals may not have the skills required to perform a task and thus learn from watching older, more experienced individuals (Schuppli et al. 2016). Alternatively, older individuals may benefit from innovations (such as new feeding methods) from younger individuals (Perry, Barrett, and Godoy 2017) or rely on the hunting efforts of younger individuals when they are no longer capable of capturing prey on their own (Ford et al. 2011). Individuals also have different energetic requirements based on their sex or reproductive state, and these requirements may dictate the prey type (Oelze et al. 2016; Carle et al. 2015), foraging habitat quality (Mackie and Racey 2007; Tennessen et al. 2019), and social behavior (Maestripieri 1994). Therefore, age, sex, and reproductive state may influence the probability of partaking in dyads and the role individuals fill.

Alternatively, kick-feeding might be a form of altruistic cooperation with indirect benefits if the actor and receiver are related. However, this is unlikely in the GOM population. Although a mother and all of her offspring will likely share

the same feeding ground throughout their lives (Baker et al. 1990; Clapham et al. 1993), most direct associations among individuals do not involve first-order kin (Clapham 1993). Furthermore, cooperation between males and females on the feeding ground is unlikely to significantly increase mating opportunities with those females. Humpback whales from different feeding populations in the North Atlantic interbreed on the same low latitude winter breeding grounds in the West Indies (Katona and Beard 1990). Since whales from many feeding grounds share the same breeding ground, there is not a high likelihood of a GOM male mating with a GOM female.

However, if the actor does not benefit (directly or indirectly) from the association and the receiver reduces the amount of prey the actor consumes, the receiver's selfishness may be the driving force behind kick-feeding dyads. In the case of selfishness, the receiver's action (engulfing a portion of the prey corralled by the kicker) is a form of competition. One would expect receivers to target the same kick feeder multiple times if they can successfully out-maneuver them, versus attempting to steal from multiple kick-feeders requiring the receiver to learn the timing of each actor’s kick-feeding sequence.

This study examined kick-feeding to determine if it is a form of cooperation. To accomplish this goal, I categorized the role (actor or receiver) individuals filled, whether those roles changed over time, and determined if a whale's demographic influenced the likelihood of filling the actor or receiver role. I hypothesized that kick-feeding is a mutually beneficial cooperative behavior.

Forms of cooperation will be exhibited when individuals either alternate the more energetically demanding role (direct reciprocity) or they pair with the same individual within and between years suggesting a greater benefit to working with a specific individual (weak altruism). However, I also hypothesized that if role exchange was not evident, then demographic influenced individuals' roles in kick-feeding dyads, therefore hindering individuals from exchanging roles. I predicted juveniles/younger whales were more likely to be receivers, but that males and females would fill both the actor and receiver roles. I also predicted that females would undertake different roles depending on if they were pregnant or lactating.

Methods

Datasets

Behavioral sequencing dataset. The Whale Center of New England (WCNE) studied the behavior of baleen whales in the southwest GOM from 1980 to 2012. WCNE developed an 80-code ethogram to categorize humpback whale surface behaviors during behavioral follows. Staff and interns conducted behavioral focal-follows per Altmann (1974) and also collected photo-identification and group association data with corresponding times and locations. This long-term research provided a basis for studying the influence of demographics on the dynamics of kick-feeding within the context of the regional population.

Although WCNE collected three decades of behavioral data, for this analysis I only used data collected during the years I was associated with the organization,

2005 to 2009. I used data collected by or under the guidance of C. Pekarcik (2005-2006) and myself (2006-2009). This subset of the WCNE behavioral follows ensured consistency of behavioral data while covering the most prolonged field effort, with an average season ranging from April 15th through October 29th across all five years. Most of these data were collected during three to four-hour whale watching trips out of Gloucester, MA, or Boston, MA, with occasional eight-hour trips from Gloucester, MA. These trips visited areas in and around Stellwagen Bank National Marine Sanctuary and Jeffreys Ledge (Figure 5). Once a year, data were collected during a 2-3 day whale watching trip that departed from Montauk, NY and collected opportunistic data east and southeast of Cape Cod, Massachusetts.

I identified kick-feeding by auditing the behavioral data. Kick-feeding varies between individuals but includes striking the surface of the water with the ventral side of the flukes (tail-flick, tail-slash, or lobtail) prior to a dive as well as striking the surface in the process of diving (fluke-lobtail or fluke/corkscrew). Before kicking, a whale can also surge out of the water and slap the ventral side of its head (chin slap) or cause a disturbance with its pectoral flippers (flipper flick). Then the whale lunges through the disturbance, sometimes with the addition of a bubble net or bubble cloud enveloping the disturbance the kick created.

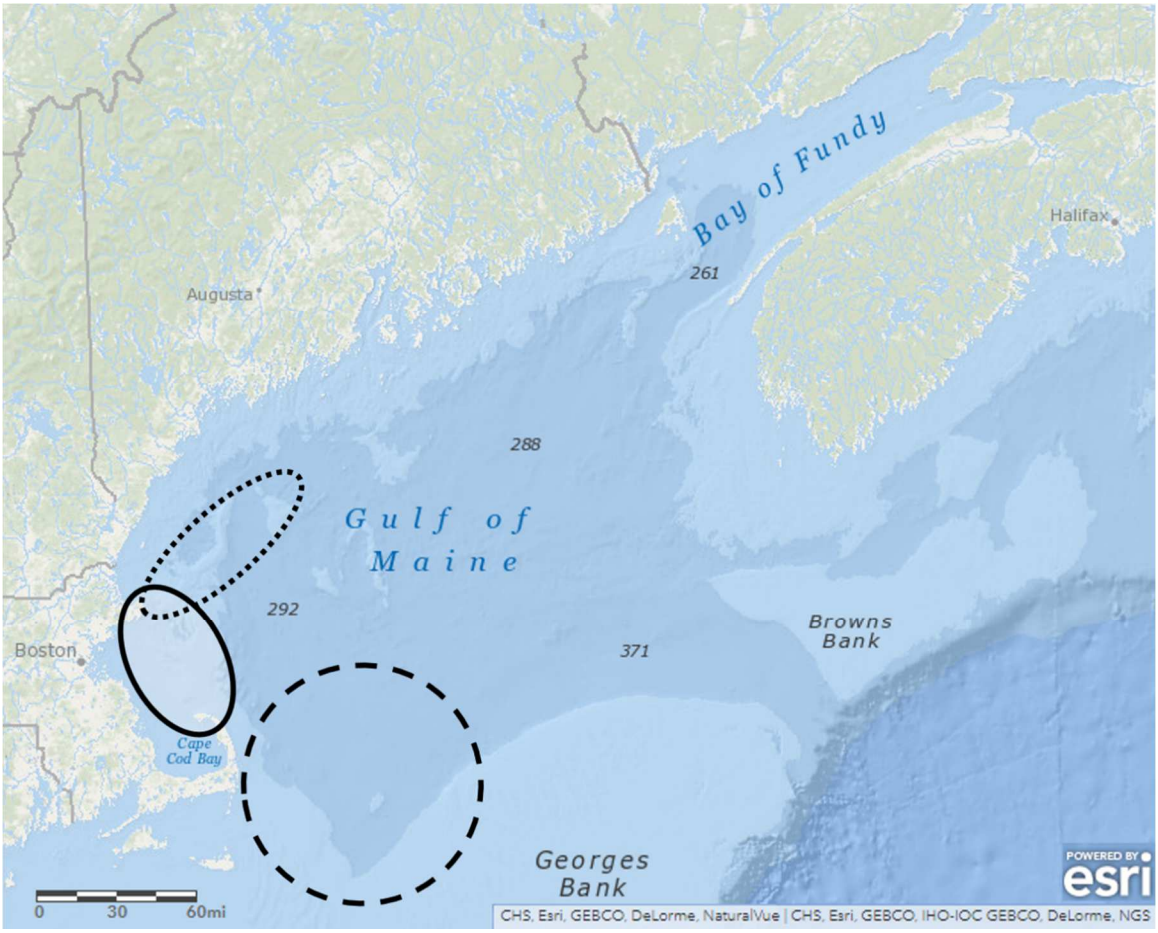

Figure 5. Areas in the southern Gulf of Maine where focal-follow data was collected. Focal-follow data collected in the southern Gulf of Maine was audited for kick-feeding behavior. The majority of effort was centered in and around Stellwagen Bank National Marine Sanctuary (solid oval). Additional effort occurred to the north on Jeffreys Ledge (dotted oval) as well as to the south between Cape Cod and Georges Bank (dashed oval).

When I identified a sequence of behaviors indicating kick-feeding, I recorded if the behavior involved a single individual (solo), a pair (dyad), or a group (3+ individuals). Each time the group members changed, or a role exchange occurred, I recorded the association as a new event. I categorized individuals in a kick-feeding group as either an actor or receiver during the auditing process. The actor was the individual that created a disturbance with its body. In contrast,

the receiver was a whale associated with the kick-feeder who lunged through the actor's disturbance. I then assessed the number of times individuals associated with each other (unique pairings) and the consistency of their roles within those pairings (unique dyads).

For events involving mother and calf pairs, the dependent calves were not included in the analysis nor included in the number of whales in the group since they were still nursing and likely not part of the prey capture process. I removed events in which there was one actor and two receivers (n = 11) due to the small sample size and the focus of this study on kick-feeding dyads. I also excluded events with two actors (n = 3) since I could not determine which disturbance the dyad lunged through based on the sequencing data, and events (n = 2) in which the individuals could not be identified (one solo and one dyad).

To understand the social context of kick-feeding, I determined the demographic class of all individuals seen during the trips audited for kick-feeding behavior, whether they kick-fed or not. This "study population" included one record for every whale each year it was seen. I compared kick-feeders to individuals who were using the same habitat, prey, and environmental conditions.

Long-term population dataset. To determine age, sex, and reproductive state for whales identified in the study population, I used demographic data from the Gulf of Maine Humpback Whale Catalog curated by the Center for Coastal Studies (CCS). CCS determined sex from molecular genetics (Bérubé and Palsbøll 1996b; 1996a; Palsbøll et al. 1992), photos of the genital slit, or calving

history (Glockner 1983). I classified individuals as adult, juvenile, or unknown using CCS data and protocols. The exact age of individuals was known for those first documented during their calf year. For whales with known exact ages, individuals were classified as juveniles if they were at least a year old but had not reached the earliest age at first calving (five years old) (Robbins 2007; Clapham 1992). Beyond age four, they were classified as adults regardless of their observed reproductive history. For whales first documented after their calf year, I applied a minimum age based on the assumption the whale was at least a year old when first seen. Whales with unknown ages were classified as adults when their sighting history length was at least four years in length. I classified the remaining whales with a sighting history of fewer than four years as unknown age-class.

The reproductive state of females was noted as lactating (La), pregnant (Pr), parous (Pa), or nulliparous (Nu) based on their sighting history and presence or absence of a calf. I classified females as lactating when they were observed with a dependent calf in the study. Females were retroactively classified as pregnant in a given year if CCS recorded them as having been seen with a calf the following year. Parous females had previously calved but did not have a calf in the year in question. Nulliparous females were at least five years old but had not yet been seen with a calf. If a lactating female was also known to be pregnant, I grouped her with other lactating females (instead of pregnant females) since

other lactating females may have also been pregnant but were not seen the following year or did not carry their fetus to full term.

Analysis

To test the hypothesis that kick-feeding is a mutually beneficial cooperative behavior based on role exchange or repeated associations, I determined the occurrence of direct reciprocity and weak altruism within my study period. I categorized kick-feeding dyads as direct reciprocity events when the same kick-feeding pair fed together within or between years and role exchange occurred. I also classified a dyad as a form of weak altruism when the same pair occurred within or between years, but no role exchange occurred.

I wanted to ensure that relatedness was not a confounding factor when assessing the benefits of associations; therefore, I used maternal relatedness to determine if kick-feeding was a form of altruistic cooperation between relatives. Close relatives were identified from lineages documented in the CCS Gulf of Maine Humpback Whale Catalog. Pairs involved first-order maternal relatives if the actor and receiver shared a mother-offspring or sibling relationship. Unfortunately, paternity data were not available for the study population; however, given the mating system of this species, most of the males fathering GOM whales are not expected to be part of the study population.

I also tested the hypothesis that demographics influenced individual roles in kick-feeding dyads, therefore hindering individuals from exchanging roles. To test this hypothesis, I compare the number of events with male and female actors in

both same-sex dyads (the actor and receiver were the same sex) and mixed-sex dyads (composed of a male and a female) using Pearson's chi-square test. I repeated the analysis between mature and juvenile whales, among the different female reproductive states, as well as if the actor was older, younger, or the same age as the receiver (age-order). When the sample size was small, and the expected cell value was less than five, I applied Fisher's exact test. I used descriptive statistics to determine if the demographics of actors and receivers differed from expected rates based on the study population or solo kick-feeders. I also determined if the occurrence of kick-feeding dyads composed of mixed or same-sex pairs differed from expected rates based on the composition of the study population or solo kick-feeders. All statistical analysis was completed in R 3.6.2 (R Core Team 2019) and RStudio (RStudio Team 2019).

Results

Cooperation

Direct reciprocity. During the five-year study period, 62 kick-feeding dyads represented 56 unique pairings of 64 unique individuals. The actors included 34 unique individuals, and the receivers consisted of 42 unique individuals (Figure 6). Even though 19% (n = 12) of individuals filled both actor and receiver roles, representing 35% of actors and 29% of receivers, only two instances of inferred direct reciprocity within or between years occurred. These instances of direct reciprocity represented 4% of unique kick-feeding pairs documented during the study (Figure 6). One involved two pregnant females who switched roles on the

same day. The other involved two parous females and they also switched roles on the same day. Nineteen percent of the whales filled both roles during the study, but 83% of those whales filled the opposite role with another whale, therefore negating any benefit they could have recouped or repaid to their original partner.

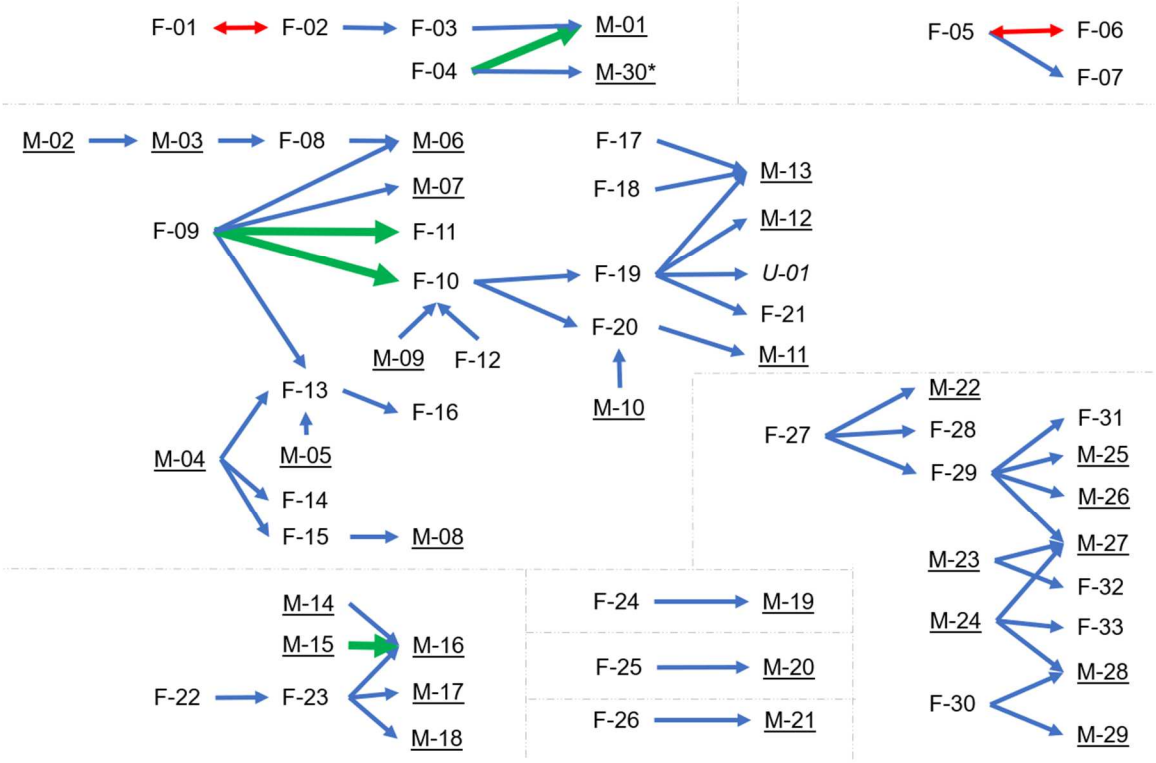

Figure 6. Flow chart of actors and receivers in kick-feeding dyads within the five-year study period. The direction of the arrow points to the animal benefiting (receiver) from the kick-feeders (actors) actions: actor → receiver. Underline individuals are males, italicizes indicates the individual with unknown sex, and * indicates the one juvenile. A blue arrow indicates a single kick-feeding dyad between two individuals. A thick green arrow indicates that dyad occurred twice with individuals filling the same roles within the same year. The two red arrows pointing in both directions indicate direct reciprocity where the individuals in the dyad switched roles. There was no instances where the same pair of whales formed a kick-feeding dyad in multiple years.

Weak altruism. During this study, none of the whales formed the same kick-feeding dyads across multiple years. Only four pairs formed the same kick-feeding dyads within the same season, and none repeated more than once. These repeated dyads represented only 7% of unique kick-feeding pairs in this study (Figure 6). Although repeated dyads were rare, many individuals were documented in multiple kick-feeding events. During the study, 38% (n = 13) of actors filled the actor's role multiple times, and 24% (n = 10) of receivers participated in more than one dyad as a receiver. Therefore, despite the lack of repeated partnerships, individuals partnered with multiple different whales during the study.

Altruistic cooperation with indirect benefits. There were 14 dyads in which the mother of both the actor and receiver was known. None of these dyads involved first-order kin (mother-offspring pair or half-siblings that shared the same mother).

Skill/Ability. Although individuals did not frequently fill both the actor and receiver role (19%), lack of ability was not necessarily the sole reason to be a receiver instead of an actor. Slightly fewer than half of the receivers (40%, n = 17) were also documented successfully kick-feeding as solo kick-feeders during the study period. Although many receivers could kick-feed successfully, fewer receivers and more actors (79%, n = 27) were solo kick-feeders than expected by random chance alone (Pearson's Chi-squared test with Yates' continuity correction, $\chi^2 = 10.142$, df = 1, p = 0.001449).

Influence of demographics

Sex. Within kick-feeding dyads, when the sex was known for both members (n = 61), the actor was more often a female (74%, n = 45) than expected, and the receiver was more often a male (52%, n = 32) than expected (Pearson's Chi-square, $\chi^2 = 8.790$, df = 1, p = 0.003, Bonferroni correction, p = 0.009 Figure 7).

The ratio of females and males filling the actor or receiver role did not significantly differ from the sex ratio found in the study population. Removing repeated sightings within years, the sex ratio of individuals documented as actors (71% female) or receivers (47% female) was not significantly different from the sex ratio in the study population (60% female) (Pearson's Chi-square, actors: $\chi^2 = 2.054$, df = 1, p = 0.152, Bonferroni correction, p = 0.456; receivers: $\chi^2 = 3.394$, df = 1, p = 0.065, Bonferroni correction, p = 0.195). Although males and females did not partake in kick-feeding dyads more or less than expected, more commonly female filled the actor role and males the receiver role.

Age-class. In kick-feeding dyads, the age of actors ranged from seven to at least 30 years old, and the ages of receivers ranged from three to at least 28 years old. Since only adult animals were actors and only one juvenile was a receiver, I cannot conclude that age-class was a predictor of whether an individual would be an actor or receiver in kick-feeding dyads (Figure 7). However, when comparing the number of unique individuals seen each year, the age-class ratio of actors (100% adult) and receivers (98% adult) did not differ from the age-class ratio of the study population (92% adult) (Fisher's Exact Test,

actor: p = 0.068, receiver: p = 0.167). Therefore, the low frequency of juveniles involved in kick-feeding does not deviate from the expected frequency based on the study population.

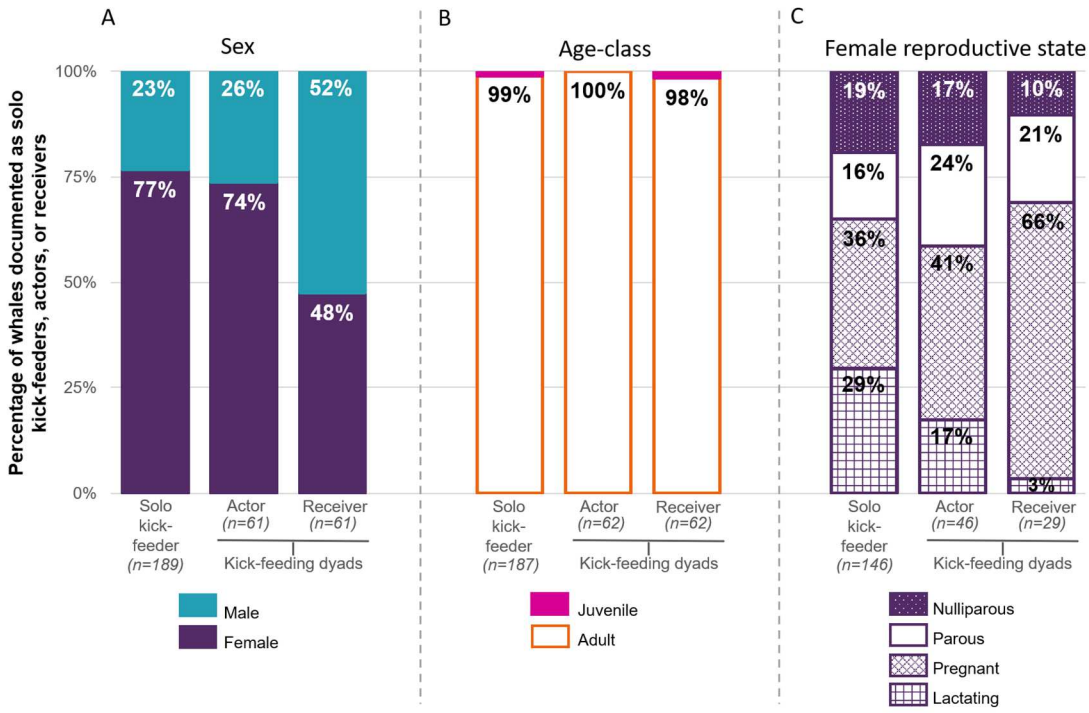

Figure 7. Comparison of sex, age-class and reproductive state of solo kick-feeders, actors, and receivers. A. Within kick-feeding dyads of known sexes, the actor was more often a female than expected, and the receiver was a male more often than expected (Pearson's Chi-square, $\chi^2 = 8.79$, df = 1, p = 0.003). The sex ratio of actors was not significantly different from the sex ratio of solo kick-feeders. **B**. Due to the small number of juveniles, it could not be determined if age-class influenced the probability of which role an individual filled. However, juveniles also filled a small percentage of solo kick-feeders. **C**. Within adult females, the ratio of reproductive states of solo kick-feeders and actors were not significantly different. The ratios of actors and receivers were not significantly different, despite lactating females only representing 3% of adult female receivers.

Reproductive state. Adult females filled the actor's role during 74% (n = 46) of the 62 kick-feeding events throughout this study. Of those 46 kick-feeding

events, 41% (n = 19) of the events had a pregnant female as the actor, with parous (24%, n = 11), lactating (17%, n = 8), and nulliparous (17%, n = 8) females filling the role of actor less often (Figure 7). Using the count of unique individuals per year as a comparison, the reproductive composition of actors (17% lactating, 43% pregnant, 27% parous, and 13% nulliparous) was not different from the reproductive composition of the study population (29% lactating, 31% pregnant, 21% parous, and 19% nulliparous) (Fisher's Exact Test, $p = 0.302$, Bonferroni correction, $p = 0.604$).

In contrast, I found a relationship between the reproductive states of receivers (5% lactating, 59% pregnant, 23% parous, and 14% nulliparous compared to the study population (29% lactating, 31% pregnant, 21% parous, and 19% nulliparous) when excluding repeated events by individuals within years (Two-sided Fisher's exact test, $p = 0.014$, Bonferroni correction, $p = 0.028$). Although the reproductive composition of actors did not deviate from expected values, lactating females were under-represented, and pregnant females were over-represented within the receiver category compared to the study population.

Dyad composition. Slightly more than half (55%) of the kick-feeding events were composed of male-female pairs (mixed-sex dyads) (n = 34), 44% were same-sex dyads (n = 27), and one dyad involved an individual of unknown sex. Mixed-sexed dyads with a female actor (n = 25) were the most common, followed by female same-sex dyads (n = 20). Mixed-sexed dyads with a male actor (n = 9) were only slightly more prevalent than male same-sex dyads (n = 7).

Since all but one whale involved in kick-feeding was an adult, I did not attempt to compare age-class to dyad composition. However, I had enough data to determine if the actor was younger, older, or the same age as the receiver for 47% (n = 29) of the events. More often than expected, the actor was younger than the receiver (n = 10) in same-sex dyads, whereas in mixed-sex dyads, the actor was older than the receiver (n = 11) (Pearson's chi-square test with Yates' continuity correction, $\chi^2 = 5.53$, df = 1, p = 0.0187, Figure 8a). However, the results for mixed-sex dyads were likely influenced by the higher percentage of events with a female actor (81%, n = 13). Therefore, regardless of the role the female plays, she was older than the male in 75% (n = 12) of the mixed-sex dyads (n = 16).

Females of all reproductive states filled the actor role in same-sex (n = 20) and mixed-sex dyads (n = 25). However, lactating and nulliparous females did not benefit from partnering with male actors during this study (Figure 8b). Despite these apparent differences based on reproductive state, the ratio of females in different reproductive states was not significantly different between actors in mixed (16% lactating, 52% pregnant, 24% parous, and 8% nulliparous) and same-sex (15% lactating, 30% pregnant, 25% parous, and 30% nulliparous) dyads (Fisher’s exact test, p = 0.2596) nor between receivers in mixed (0% lactating, 78% pregnant, 22% parous, and 0% nulliparous) and same-sex (5% lactating, 60% pregnant, 20% parous, and 15% nulliparous) dyads (Fisher’s exact test, p = 0.788). Thus, there was no substantial influence of reproductive

states on females' roles in same-sex or mixed-sex kick-feeding dyads, even though lactating and nulliparous did not fill the receiver role in mixed-sex dyads.

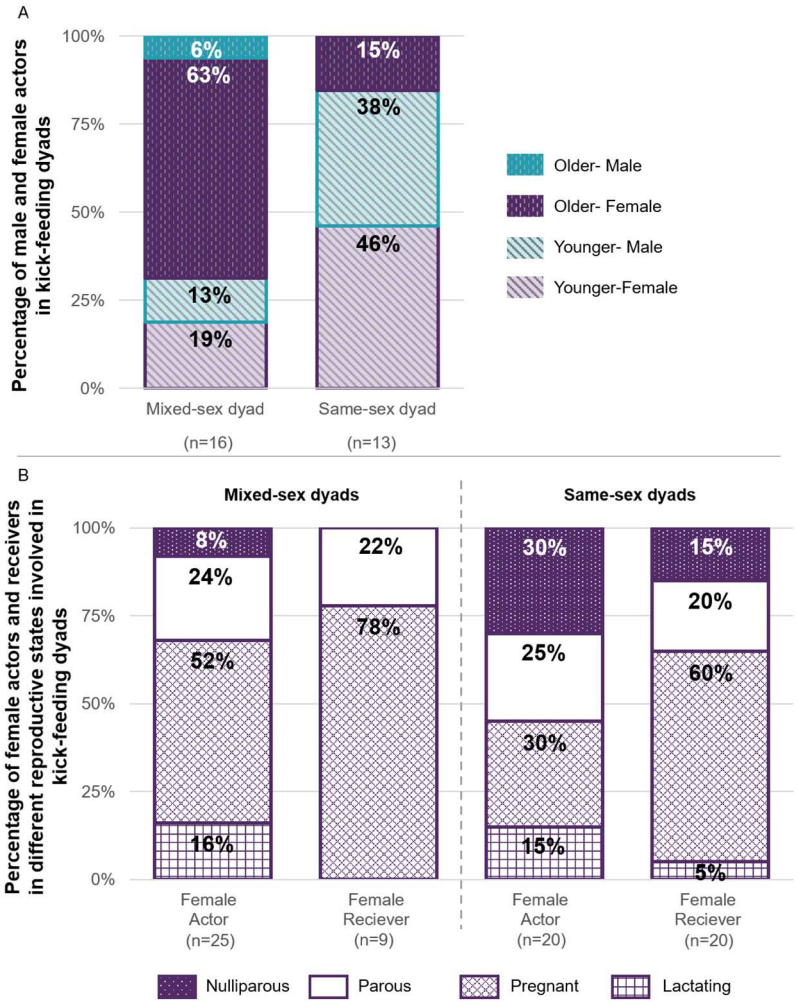

Figure 8. The percentage of males and females in mixed- and same-sex kick-feeding dyads. A. In mixed-sex dyads the actor was older than the receiver (n = 11) whereas the actor was younger than the receiver (n = 10) in same-sex dyads more often than expected by random chance alone (Pearson's chi-square test with Yates' continuity correction, $\chi^2 = 5.53$, df = 1, p = 0.01868). Additionally, the female was older than the male in 75% (n = 12) of the mixed-sex dyads (n = 16), regardless of the role she filled. **B.** The ratio of females in different reproductive states filling the actor or receiver role in mixed- and same sex- dyads did not significantly differ. Although females in all reproductive states filled the actor role in same-sex and mixed-sex dyads, no lactating or nulliparous females ever filled the receiver role with male actors.

Discussion

This study tested two hypotheses. 1) Kick-feeding is a mutually beneficial cooperative behavior and 2) If direct reciprocity was not evident, then demographic influenced individuals' roles in kick-feeding dyads, therefore hindering individuals from exchanging roles. The results did not indicate that kick-feeding whales were cooperating during this study. However, the results suggest that demographics, along with the broader population structure, influenced which roles individuals were likely to fill.

Cooperation

Direct reciprocity. The results of this study did not support the hypothesis that kick-feeding dyads are a form of mutually beneficial cooperation. Only 6% (n = 4) of unique individuals involved in kick-feeding exhibited behavior inferred as direct reciprocity, and role exchange only occurred once for each pairing. It is possible that the benefit of partnering with a specific individual did not outweigh the cost of searching for or staying with that individual for an extended period of time until the prey formation was suitable for kick-feeding**.** Additionally, direct reciprocity requires individuals to recognize and remember short interactions with individuals within and across years. More social odontocetes can recognize and keep track of individuals across years (Sayigh et al. 1999), but this cognitive ability has not been fully explored for humpback whales. The occurrence of some long-term associations (Ramp et al. 2010b; Sharpe 2001) and evidence of preferred associates by some whales (Tackaberry and Robbins 2017) suggest

humpbacks have the ability to recognize individuals across multiple years, yet the majority of whales choose to have short, fluid associations.

Weak altruism. Weak altruism was also not suggested by the dynamics of kick-feeding dyads. Even if actors did not gain as much benefit as receivers, as long both individuals benefited from the pairing (weak altruism), I would have expected repeated instances of the same dyads. However, the same dyads never occurred between years during this study, and only 7% (n = 4) of the unique pairs occurred twice within the same year. The lack of repeated associations between individuals in this study suggests that the actors and receivers did not benefit from the association enough to prefer specific pairings over random pairings, whether individuals fill the same (weak altruism) or different roles (direct reciprocity). Again, it is probably more costly for a whale to keep track of its successful partnership and search for those whales than randomly pair with other kick-feeders.

Altruistic cooperation with indirect benefits. Although an assessment of all of the long-term indirect benefits of kick-feeding dyads was outside of the scope of this study, it was apparent that first-order kin were not favored in dyads. This lack of close relatedness between actors and receivers agrees with previous findings that most associations on the feeding ground do not preferentially involve close relatives (Clapham 1993), despite maternally driven site fidelity to feeding grounds (Katona and Beard 1990; Baker et al. 1990; Clapham et al. 1993; Palsbøll et al. 1995; Clapham and Mayo 1987). Future research focusing

on the age of first reproduction, fecundity, and offspring survival/fecundity will help determine if actors obtain long-term indirect benefits or increased inclusive fitness by kick-feeding with other individuals.

Skill/Ability. It was not necessarily a lack of skill causing individuals to be receivers rather than actors. Forty percent of receivers were also documented solo-kick-feeding. Therefore, even though almost half of the receivers had the necessary skills to be actors, they filled the receiver role instead. This suggests there are benefits of the receiver role, or possibly, that whales outcompeted by other kick-feeders are forced into the receiver role.

More research is needed to determine how much prey is engulfed by the actor and receiver and how prey patch size influences the surface feeding method. Within kick-feeding, an increase in group size may not increase the amount of food available per group member in the same way that cooperative pack-hunting is hypothesized to mutually benefit each group member (Bailey, Myatt, and Wilson 2013; Boesch and Boesch 1989). Although the environmental factors that affect the choice of feeding technique are still not well-understood, kick-feeding may be most effective when the prey is composed of small patches. If so, then the size of the disturbance created by a single actor could limit the number of other individuals that could potentially benefit.

Influence of demographics

The results of this study suggest that there is not strong evidence for cooperation, nor individual preferences for kick-feeding partners. Therefore, for

the rest of the discussion, I assume that the opportunity to form kick-feeding dyads was created when a whale finds a prey patch that another whale is already consuming through kick-feeding. When a whale encounters another individual solo kick-feeding, it must either directly compete with them by feeding next to it, join the kick-feeder as a receiver, or choose not to feed on that prey patch.

I would expect same-sex female dyads to be the most prominent dyads based on the female-biased sex ratio in the study population (1.5 females for every male) and throughout the southern GOM (Robbins 2007). However, the results from this study suggest that more dyads were mixed sex with females being the actors. Therefore, this study's results did not support the expectation that the demographic structure of the underlying population was solely responsible for the dyad composition. Some could interpret these results as females having a behavioral preference to be actors and males to be receivers. However, instead of individuals preferring to fill different kick-feeding roles based on their sex, the avoidance of specific associations based on sex and reproductive state may be an alternate explanation.

Sex. Even though antagonistic behavior is rare between males on the feeding ground, males tend to associate with females (Clapham 1993; 1994; Weinrich and Kuhlberg 1991). The results of this study support previous studies that males prefer to associate with females since mixed-sex dyads (n = 34) were much more prevalent than same-sex male dyads (n = 7). The higher frequency of male

association with females in a female-biased population helps explain the skew of kick-feeding dyads towards mixed-sex dyads with male receivers.

Age-class. Unfortunately, I could not address the prediction that juveniles are more often receivers. The results of this study were inconclusive about the influence of age-class on kick-feeding dyads. However, the small proportion of juveniles documented as actors (0%) or receivers (2%) does not significantly differ from the percentage of juveniles in the study population (8%) or the percentage of solo kick-feeders composed of juveniles (2%). Therefore, even though only adults filled the actor's role, that does not mean that juveniles necessarily avoid or cannot fill the role. Due to the smaller proportion of juveniles in the overall population, sightings data from a longer study period is needed or a concerted field effort to seek out and observe that age-class.

Reproductive state. An adult female's reproductive state has previously been shown to influence her association preferences. Lactating females are less likely to associate with other adult whales on the feeding grounds (Clapham 1994; 1993; Sardi, Weinrich, and Connor 2005; Ramp et al. 2010b; Clapham and Mayo 1987; Clapham 2000). When they do associate with another whale, it tends to be an adult male (Sardi, Weinrich, and Connor 2005). In contrast, pregnant females tend to have longer associations than lactating females or adult males (Ramp et al. 2010b; Weinrich 1991). The results of this study suggest that a female's reproductive state influences her preference for or avoidance of kick-feeding dyads. The fewer than expected lactating female receivers during this

study highlights their lower likelihood of joining with other whales. The lower frequency with which lactating females and adult males choose to associate with specific demographics leaves more opportunity for pregnant females to join solo kick-feeders (explaining the over-representation of pregnant female receivers) or to continue kick-feeding when another whale attempts to form a dyad with them.

Dyad composition. In kick-feeding dyads, adult actors were younger than the receivers in same-sex dyads, whereas actors were older in mixed-sex dyads. Additionally, adult females were more often older than adult males, regardless of their role, in mixed-sex dyads. Since my study spanned a wider range of adult ages than previously published work (Weinrich 1991; Weinrich and Kuhlberg 1991; Clapham 1994), I cannot determine if the age structure of kick-feeding dyads was unique to this feeding method or also common in non-kick-feeding associations. However, the southern GOM has a higher percentage of adult females and juveniles than the northern GOM, which has a higher percentage of adult males (Robbins 2007). As females age in the southern GOM, there may simply be fewer male conspecifics her age or older in a given aggregation and a higher proportion of younger adult males. Therefore, the southern GOM population structure provides a logical explanation for why mixed-sex kick-feeding dyads tend to be composed of older females with younger males.

Conclusion

The influence of non-ecological factors, such as demographics (age, sex, and reproductive state), on coordinated and cooperative behavior can be challenging

to address in wildlife and particularly cryptic species. Since elements of coordination can be seen at the surface, kick-feeding in humpback whales represents a collaborative coordinated behavior within which the influence of demographics on feeding group composition can be determined.

This study suggests that although kick-feeding is a collaborative coordinated behavior, it does not appear to be a form of cooperation. More likely, kick-feeding dyads are a product of competition (selfishness of the receiver) or created by random interactions caused by prey distribution. The lack of role exchange between pairs and the absence of repeated association between years indicate that any benefit to partnering with the same individual does not outweigh the benefit of forming a dyad through random interactions. Additionally, it appears that males and lactating females are less likely to be receivers, possibly due to male-male avoidance and the lower sociability of lactating females. These preferences apparently overshadow benefits gained from joining a kick-feeder. Therefore, both individual demographics and the broader population structure influence which roles are available to individuals in kick-feeding dyads.

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